CONDITIONS FOR COEXISTENCE OF POTENTIAL COMPETITORS IN MARINE PSAMMOPHILOUS CILIATES COMMUNITY

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ABSTRACT. The distribution of three pairs of taxonomically closely related species of psammophilous ciliates (*Tracheloraphis incaudatus, Tr. phoenicopterus, Remanella margaritifera, R. rugosa, Histobalantium majus, H. marinum*) was studied in the intertidal zone of the White Sea. Because the values of overlap between trophic niches, estimated by Pianka's index, were especially high for the species of the same genus (0.94 for the pair of *Tracheloraphis* species, 0.94 for that of *Remanella*, and 0.96 for *Histobalantium*), the study was aimed to find condition that determine the coexistence of these species. The most important is the separation corresponding to different vertical distribution in the sediments (along the gradient of redox-potential); less important is the separation in time. Presumably there is no appreciable separation of closely related species by differences in micro-scale distribution on horizontal plane. The overlap between distributions of species from one pair along one of spatial dimensions is inversely related to the total density of both species. In three-dimentional space, this dependence is more complicated. Complete species separation corresponds to specific density values. Rank of a species in the community is determined by its ability to compete for food and space. Among species of the same genus, the dominant competitor is the species characterized by smaller value of overlap with the rest of species of the community (i.e. less affected by the pressure of diffuse competition) and inhabiting the upper, closer to the photic zone, layer of sediment.

Key words: interspecies competition, diffuse competition, coexistence, trophic niche, psammophilous ciliates, spatial and temporal distribution.

One of the problems, which has been drawing an increasing attention of ecologists for a long time is that of interspecies competition. Successful analysis of this type of interactions under the field conditions, where an individual organism is affected by many factors hardly controlled by investigator, depends to a large extent on correct choice of appropriate community and spatial-temporal scale for study. In our opinion, the community of marine psammophilous ciliates is highly perspective for such studies.

The basic organizing principle of psammophilous community consisting of many different species is the complementary utilization of ecological resources (Burkovsky 1984). In each locus of habitat and in each moment of time, there is such a combination of species which ensures their minimum feeding overlap. This complementary spatial-temporal distribution, which is a consequence of interactions between the species themselves and between the species and their environment, reduces the competition.

In complex natural community where each species interacts with great number of others (sometimes these contacts are accidental due to the patchy distribution of organisms), the competition has a "diffuse" nature (Pianka 1974, Schoener 1974, etc.). The contribution of every species to the total competition is relatively small and depends on many factors, particularly on species density and the amount of available food. Competition is evidently stronger in the case of closer trophic niches of interacting species. In such multispecies community as marine psammon, there are many species with considerably overlapping feeding spectra. Usually these species are closely related (they are often congeneric).

The aim of present paper is to study conditions which provide coexistence of potential competitors among psammophilous ciliates by the analysis of their spatial-temporal interrelations.

Material and methods

Samples were collected on flat sandy beach extended in Chernaya Inlet (Kandalakshsky Bay, the White Sea) in May-September 1987.

We chose for the analysis three pairs of species with markedly overlapping trophic niches: *Tracheloraphis incaudatus — Tracheloraphis phoenicopterus, Remanella margaritifera — Remanella rugosa* and *Histobalantium majus — Histobalantium marinum*. In late summer, these species comprise more than 80% of total community biomass. Taking into account that ciliates are able to perform active diurnal and tidal migrations, the samples were taken at the same time (10.00-11.00 a.m.) and at the same phase of tide (at low water) every two weeks. Samples were taken by a glass tube (25 cm^2 in cross-section) at the depth of sand of 5 cm. As it has been shown by preliminary data, more than 95% of ciliates occur in this layer.

Sampling was carried out by two schemes. In the first case, material was collected at 26 permanent stations regularly placed within rectangular area (40×80 cm) in intertidal zone. Each sample represented one column up to the depth of 3 cm. These data were then used for the analysis of spatial-temporal distribution of ciliates on the plane of littoral. In the other case, samples were taken simultaneously from strictly fixed area (25×25 cm) located at the boundary between lower and middle parts of intertidal zone. For this purpose, 4 equal columns of sand were taken by the same glass tube, then each column was divided into 4 layers: 0-0.5, 0.5-1, 1-2, 2-3 cm. Thus, we obtained 16 separate but closely adjoining samples which form together a parcel of total volume of 30 cm^3 (3.2×3, 2×3 cm). Treated individually, these samples allowed to study the horizontal microdistribution of ciliates (in relatively homogeneous environment), the vertical one (along the gradient of environmental factors) and in three dimensional space. It is important that the scale of this study corresponded to home ranges of individual psammophilous organisms and their real interrelations with each other.

To extract ciliates from sand, the samples were washed several times with filtered sea water. After this procedure animals were totally counted under light microscope.

Simultaneously with the sampling, a number of environmental parameters were measured: redox-potential (Eh), acidity (pH), concentration of oxygen, total organic carbon ($C_{org.}$), temperature, salinity and granulometrical composition of the sand.

The overlap between species was estimated by the Pianka index (it varies from 0 to 1):

$$a_{ij} = \frac{\sum P_{ik} \cdot P_{jk}}{\sqrt{[\sum P_{ik}^2 \cdot \sum P_{jk}^2]}},$$

Where P_{ik} is the portion of resource category k (food, space, time) utilized by species i or j in the case P_{jk}.

The feeding overlap of a species (i) with the rest of community was estimated in the same way. In this case, the rest of community (more then 40 species) was considered as a species j.

Trophic niche and position of potential competitors in the community

Psammophilous ciliates feed on various items, but the bulk of their food consists of unicellular algae, bacteria and protozoans. *Tracheloraphis incaudatus* and *Tracheloraphis phoenicopterus* mainly consume large diatoms and peredineans; *Remanella margaritifera* and *R. rugosa* use small diatoms; *Histobalantium majus* and *H. marinum* have wide feeding spectra including peredineans, diatoms, bacteria and protozoans. The former four species can obviously be referred to mesophagous animals, because only one food category prevails in their diet comprising more than 50% of total food volume. Two latter species are polyphagous and it is impossible to determine any dominant food in their diet. The diet of

Table 1. Feeding spectrum overlap between potential competitors and between a species and the rest of community.

Tr. inc.	*Tr. ph.*	*R. m.*	*R. r.*	*H. mar.*	*H. maj.*	
1.00	0.94	0.05	0.07	0.12	0.10	*Tr. incaudatus*
0.14	1.00	0.09	0.09	0.34	0.12	*Tr. phoenicopterus*
	0.23	1.00	0.94	0.12	0.12	*R. margaritifera*
		0.17	1.00	0.14	0.14	*R. rugosa*
			0.25	1.00	0.96	*H. marinum*
				0.28	1.00	*H. majus*
					0.22	

Remarks. Coefficients for overlap between each of studied species and the total trophic spectrum of community are given on the main diagonal.

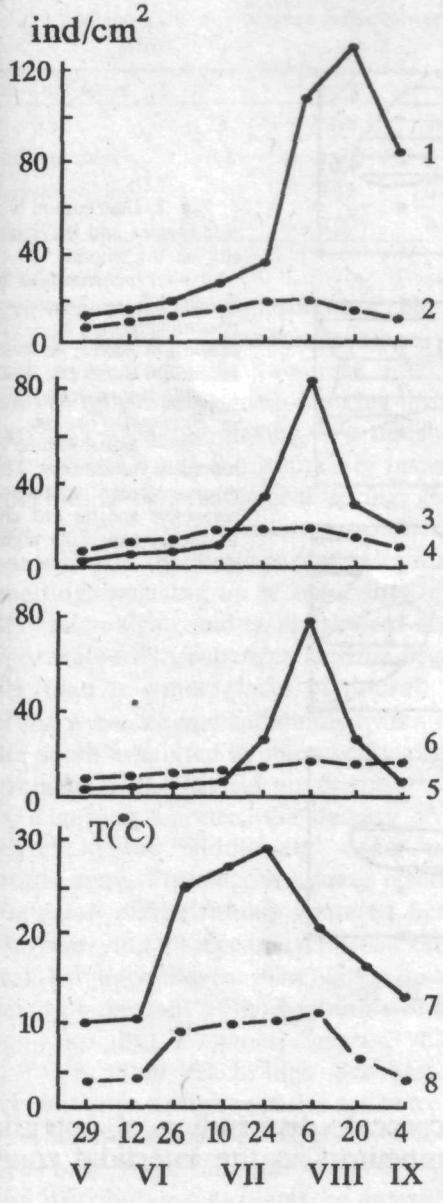

Fig. 1 Growth of populations of potential competitors in summer 1987. 1 — *Tracheloraphis incaudatus*, 2 — *Tracheloraphis phoenicopterus*, 3 — *Histobalantium majus*, 4 — *Histobalantium marinum*, 5 — *Remanella margaritifera*, 6 — *Remanella rugosa*, 7 — maximum temperature, 8 — minimum temperature. Each point on the plot is the mean value for 30 samples.

these species depends on available food in the environment to ever greater degree than the diet of all other species (Burkovsky et al. 1980, Burkovsky and Epshtein 1982). Table 1 contains data on overlap of feeding spectra of species between themselves and between a species and the whole community. These data demonstrate feeding specialization and position of each ciliate species in the trophic structure of community.

Species of the same genus have the highest coefficient values. In fact, such species are trophically very close, and they are the most probable competitors under conditions of food deficiency. In complex natural community, each species can compete with others, and the greater is the total density of animals and the smaller is the amount of available food, the stronger is that competition.

In theory, the most abundant species should be potential competitors. But as it was shown earlier (Burkovsky 1984, 1987), dominant species usually differ in food, and the competition between them, if any, might be only that for space in the case of high population density. There is no generally accepted opinion concerning the role of competition of the second, third, ... n-order. Vandermeer (1969, 1970) has demonstrated that population density does not essentially influences the results of competition between principal competitors. However, it was shown in other experiments, that the outcome of competition of higher order depends on species used in laboratory experiment: additional species may either intensify or reduce the effect of competition between main partners (Hairston et al. 1969).

In natural multispecies community, it is important to take into consideration the total pressure of competition which can be evaluated by an overlap between feeding spectrum of a single species and that of the rest of community. As it was shown earlier (Burkovsky 1984, 1987), there is a negative relation between this parameter and the abundance of a species. As it follows from the Table 1, dominant species of ciliates significantly differ by this value. This means that these species occupy unequal positions in competing community. *Tracheloraphis incaudatus* is exposed to minimum competing pressure of the rest part of community (a_{ij} = 0.14), *Remanella margaritifera* follows it (a_{ij} = 0.17), then follows *Histobalantium majus* (a_{ij} = 0.22). These species practically do not compete between themselves for food, and this circumstance presumably determines their high abundance. At final stage of seasonal succession, these species form the core of community comprising 60-80 % of total biomass. *Tracheloraphis incaudatus* is the persistent leader at this stage of succession. Species taxonomically most closely related to those dominating at the end of succession are characterized by essentially higher values of coefficient of overlap both between themselves (a_{ij} = 0.07-0.34) and with total feeding spectrum of community (a_{ij} = 0.23-0.28). This circumstance influences their competitive ability and predetermines the secondary positions of these species in the community.

Distribution of potential competitors in time

The dynamics of ciliate density during the

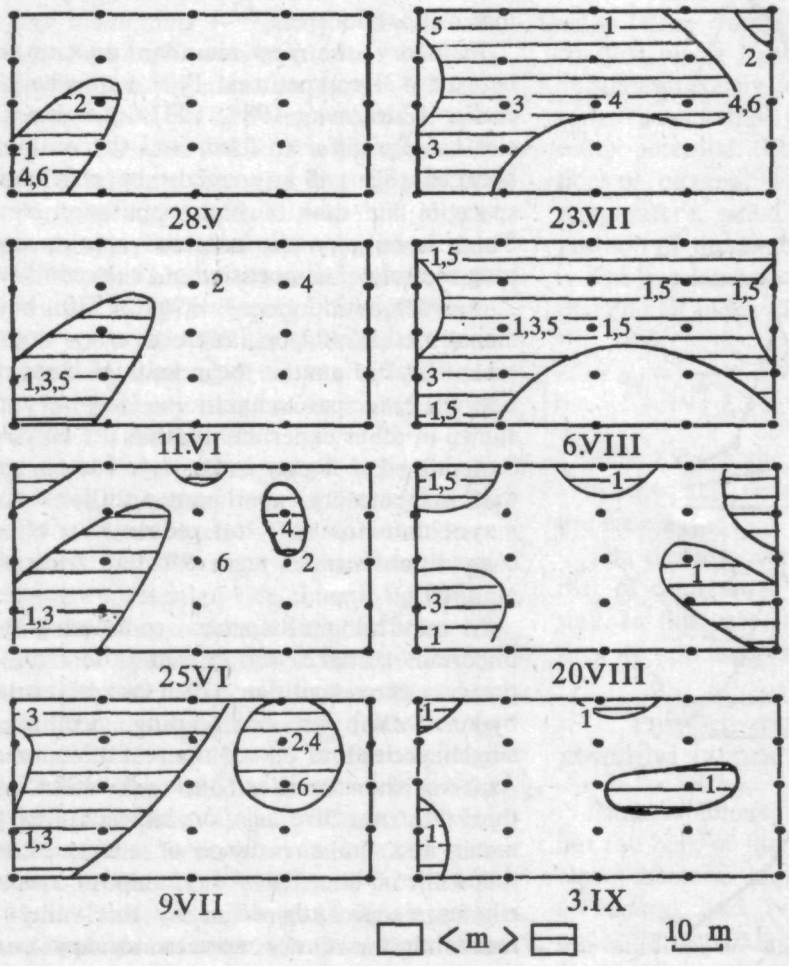

Fig. 2. Distribution of separate species and the total density on the littoral.
1 — *Tracheloraphis incaudatus*; 2 — *Tracheloraphis phoenicopterus*; 3 — *Histobalantium majus*; 4 — *Histobalantium marinum*; 5 — *Remanella margaritifera*; 6 — *Remanella rugosa*.
m — mean value. Points represent the stations. The numbers represent stations where respective species are characterized by especially high density.

growing period is shown in Fig. 1. Curve courses correspond to fluctuations of temperature, first of all to its minimum values, and to the range of diurnal variations. All species reach their maximum densities in the period when the temperature of sand within a day does not fall below 10° C and when the temperature fluctuations do not exceed 8-10° C.

The most rapid growth of the population density of *Tracheloraphis incaudatus, Remanella margaritifera*, and *Histobalantium majus* was recorded at the temperature about 29° C (maximum). Such growth continues for several weeks. *Tracheloraphis phoenicopterus, R. rugosa* and *H. marinum* had significantly lower but constant population growth rates during the most part of summer. Maximum densities of these species did not reach 20 ind/cm^2, however in early summer they were higher than those of principal competitors. It is important to note that the complete exclusion of one species by another does not occur. Potential competitors permanently coexist in time, and this circumstance should undoubtedly affect their spatial distribution.

Macroscale distribution of potential competitors in the intertidal zone

The studied plot of 320 m^2 in area is extremely great in comparison with home ranges which do not exceed 1 cm^3 for psammophilous ciliates (Burkovsky 1984). Just in these limits, individuals are able to move actively and to interact with other organisms of the psammon. 26 stations disposed on investigated area are from 10 to 90 meters apart, and thus they provide information concerning various local conditions in the community. Since the distances between stations prevent direct contacts between species of corresponding loci, these local states (samples) may be considered as relatively independent elements of the whole community. An integrity of community is maintained by general successional process embracing the whole community rather than by environmental homogeneity which is never complete. Various loci of a biotope (stations, samples) may evidently correspond to different stages of seasonal succession. Restoration of community structure that begins in spring after

Table 2. Distribution overlap between potential competitors under the area of 320 m^2 (macrodistribution)

Pairs of species	Date and values of overlap coefficients								
	28.5	11.6	26.6	9.7	23.7	6.8	20.8	3.9	Mean
Tracheloraphis	0.80	0.50	0.60	0.45	0.71	0.94	0.74	0.67	0.68
Histobalantinum	0.58	0.57	0.25	0.44	0.23	0.10	0.22	0.36	0.35
Remanella	0.47	0.90	0.59	0.24	0.42	0.68	0.41	0.52	0.53

long winter resembles the process of colonization of vacant territory. Consecutive stages of this process estimated with two-week interval are shown in Fig. 2. Specimens, occurring throughout the studied area but having low density (less than 1 ind/cm^2) are the sources of invasion. At the beginning of hydrological spring, the most suitable conditions for ciliate reproduction appear initially in the lower part of intertidal zone. Ice-melting, warming up of sediments, development of microalgae, and establishment of comparatively stable hydrochemical regime begin here earlier than in other places of littoral. At this time, the shore ice and sediments frozen through all the depth inhabited by microbentic organisms still remain in the littoral upper zone.

As it getting warmer, the density of ciliates increases in the middle and upper parts of intertidal zone. This increase takes place due to reproduction of individuals wintered here, and due to carrying of organisms from the lower littoral by tidal waves. The latter process is especially important at the beginning of growing season. Initially, *T. phoenicopterus*, *R. rugosa* and *H. marinum* reach high densities everywhere, but later on these species are outcompeted by *Tracheloraphis incaudatus*, *Remanella margaritifera* and *Histobalantium majus*.

The distribution of ciliates on intertidal plot is so irregular that it is impossible to analyze it cartographically in details. However the similarity (or dissimilarity) in the distribution of species can be estimated with the aid of Pianka index of interspecies overlap (under the area of 320 m^2) (Table 2).

As we can see, overlap coefficients for each pair of species are inconstant, they vary considerably throughout the summer. This variability indicates the instability of balance between coexisting species. *Tracheloraphis* pair of species has the highest overlap coefficients while *Histobalantium* pair has the lowest ones. This evidences not only the degree of similarity in multidimensional niches of corresponding species, but also different (higher in the former case and lower in the latter one) probabilities of coexistence of these species under given conditions. The coexistence probability is determined by availability of appropriate food, presence of other competitors, and other factors.

Microscale distribution of potential competitors in the intertidal zone

The data obtained allow us to estimate the distribution of ciliates in three different ways: on the horizontal plane, along the vertical profile in the column of sediments, and in three dimensional space. Distribution of potential competitors on the horizontal plane (under the area of 10 cm^2) as a matter of fact is the distribution of individuals in relatively homogeneous environment. Using this scale, we failed to find out any significant differences in distribution of Eh, pH, O_2 and $C_{org.}$ The homogeneous environment provides a limited possibility for divergence of related species in space. If there are some differences in their distribution, they may be related to randomly fluctuating factors. Indeed, as it follows from the data below, the overlap coefficients for potential competitors are higher in this case than in the case of macroscale distribution in the whole intertidal zone on area of 320 m^2.

Values of spatial overlap in both cases of micro- and macrodistribution vary for different pairs of species independently of each other and of the stage of seasonal succession. This indicates the prevalence of stochastic mechanisms in maintaining the balance between species. All species

Table 3. Distribution overlap between potential competitors under the area of 320 m^2 (microdistribution)

Pairs of species	Date and values of overlap coefficients								Mean	Mean without 29.5
	29.5	12.6	27.6	10.7	24.9	5.8	21.8	4.9		
Tracheloraphis	0.17	0.99	0.93	0.84	0.96	0.85	0.95	0.83	0.84	0.94
Histobalantium	0.15	0.90	0.63	0.95	0.52	0.90	0.77	0.70	0.69	0.76
Remanella	0.37	0.98	0.54	0.82	0.96	0.66	0.69	0.76	0.73	0.78

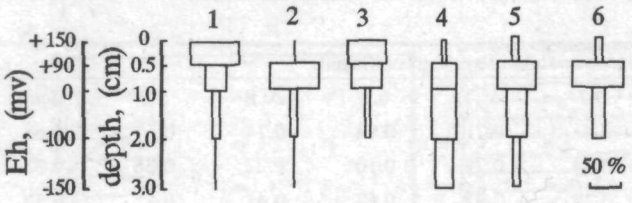

Fig. 3. Vertical distribution of potential competitors in 0-3 cm layer (mean seasonal values).
1 — *Remanella margaritifera*; 2 — *Remanella rugosa*; 3 — *Histobalantium majus*; 4 — *Histobalantium marinum*; 5 — *Tracheloraphis incaudatus*; 6 — *Tracheloraphis phoenicopterus*

have minimum overlap in homogeneous environment in spring, i.e. in the period when their population densities just begin to increase. In this case, the low values of overlap coefficients are not the result of strong interactions between related species, but reflect a slim chance of coincidence of populations with low density (less than 1 ind/cm^2). As populations become numerous, the overlap between them increases, and two weeks later their distributions in space become coincident.

Potential competitors are vertically distributed within sediments along the gradient of a set of environmental factors, the most principal among them being oxygen, redox-potential (Eh), acidity (pH), and presence of food. Vertical distribution of related species (mean seasonal value) in 0-3 cm layer and respective values of redox- potential (Eh), which is an integral parameter of environment, are shown in Fig. 3. Considerable part (more than 75 %) of populations of potential competitors is concentrated in the surface 3 cm layer of sand (where Eh > 0). However, even within this thin layer, the species diverge remarkably along the redox-gradient. *Remanella margaritifera* and *Histobalantium majus* take up the most upper position, *Tracheloraphis incaudatus* and *Histobalantium marinum* occupy the lowest one. Such distribution patterns is maintained throughout the summer. It is disturbed only in some periods of diurnal activity of ciliates connected with their feeding and competition for space. The values of coefficients for overlap between potential competitor distributions within sediments are given in Table 4.

As in the previous case, the highest overlap is characteristic of *Tracheloraphis* species while lowest one is recorded for *Histobalantium* species. Corresponding values vary from 0.62 to 0.99 for the former pairing and from 0 to 0.92 for the latter one. *Remanella* species occupy an intermediate position. Thus, the relative disposition of *Histobalantium* within sediments is more variable than that of *Remanella* and, all the more, *Tracheloraphis*, which are limited by the same sediment volume. Low mean value and high variability of the coefficient characteristic of *Histobalantium* indicate strong interactions between species in the process of maintaining the balance as well as some "difficulties" of coexistence of these species. It should be emphasized here that variations in mutual disposition of related species took place against a background of practically stable redox-profile, i.e. this variations were not connected with abiotic factors.

Distribution of potential competitors in three dimensional space gives a real presentation of mutual disposition of populations and real interactions between them. The data concerning the distribution overlap between potential competitors in a volume of 30 cm^3 are given below.

Principal pattern of species distribution at this

Table 4. Distribution overlap between potential competitors within sediments in 0-3 cm layer.

Pairs of species	Date and values of overlap coefficients								Mean
	29.5	12.6	27.6	10.7	24.7	5.8	21.8	4.9	
Tracheloraphis	0.62	0.77	0.90	0.98	0.99	0.91	0.73	0.85	0.87
Histobalantium	0.93	0.52	0.47	0.10	0.00	0.29	0.00	0.30	0.30
Remanella	0.79	0.71	0.80	0.20	0.57	0.53	0.38	0.58	0.59

Table 5. Distribution overlap between potential competitors in three dimensional space (in a volume of 30 cm).

Pairs of species	Date and values of overlap coefficients								Mean	Mean without 29.5
	29.5	12.6	27.6	10.7	24.9	5.8	21.8	4.9		
Tracheloraphis	0.07	0.65	0.72	0.82	0.76	0.72	0.62	0.84	0.66	0.74
Histobalantium	0.14	0.29	0.27	0.04	0.00	0.11	0.00	0.10	0.12	0.12
Remanella	0.36	0.37	0.48	0.22	0.47	0.38	0.28	0.35	0.36	0.36

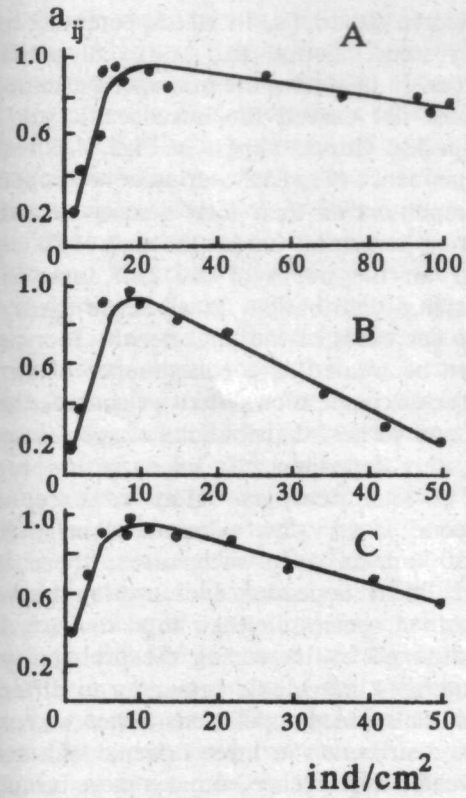

Fig. 4. Dependence of spatial overlap of potential competitors on their total density (by data on the species horizontal distribution under the area of 10 cm^2).
A — *Tracheloraphis* species, B — *Histobalantium* species, C — *Remanella* species.

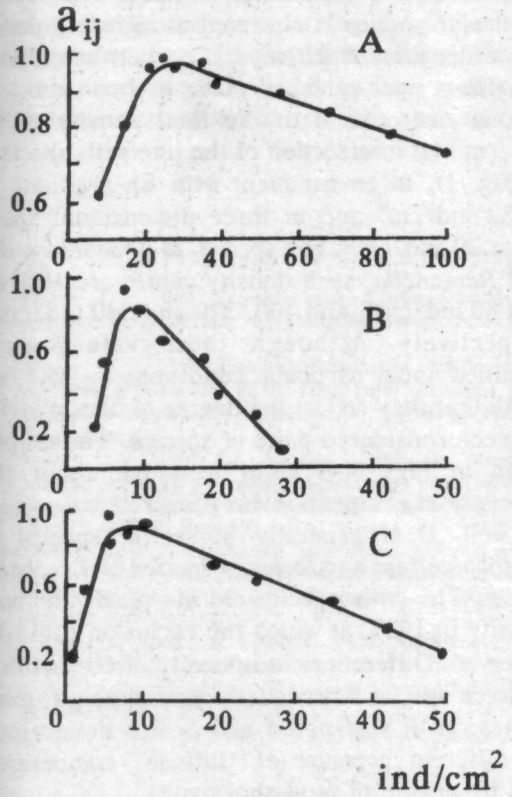

Fig. 5. Dependence of spatial overlap of potential competitors on their total density (by data on the species vertical distribution within sediments).
A — *Tracheloraphis* species, B — *Histobalantium* species, C — *Remanella* species.

scale reflect the peculiarities of distribution on vertical and horizontal planes. But there are more possibilities for species segregation in three-dimensional space than along each axis of space taken separately. *Tracheloraphis* species are characterized by the highest values (0.74) while *Histobalantium* species have the lowest ones (0.12); *Remanella* species take up an intermediate position (0.36). Thus, coexistence of related species in a volume of 30 cm^3 takes place due to corresponding space resource partitioning between them. Seasonal variations of interspecies overlap, showing an ability of related species to maintain the equilibrium, are the same in all three pairs of species. This means that in three-dimensional space potential competitors reach the equilibrium by coordinated changes in their relative positions. It is most probably that ciliates regulate their interrelations by active movement in space, as it has been revealed in the study on diurnal vertical migrations of these species (Burkovsky et al. 1983).

Although the overlaps between feeding spectra of studied pairs of species are very similar (a_{ij} = 0.94-0.96), spatial overlaps between all these pairs remarkably differ (a_{ij}: 0.74, 0.36, 0.12). These differences can be explained by

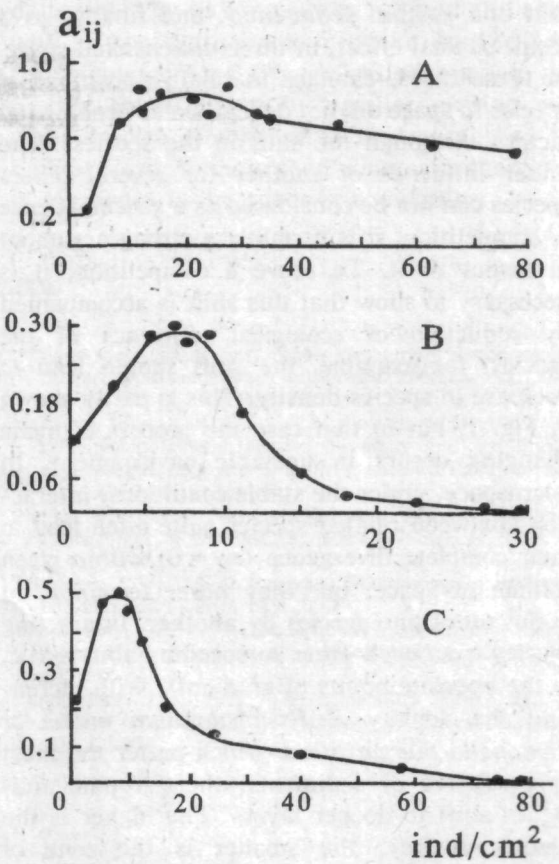

Fig. 6. Dependence of spatial overlap of potential competitors on their total density (by data on three-dimensional distribution of the species in a volume of 30 cm^2).
A — *Tracheloraphis* species, B — *Histobalantium* species, C — *Remanella* species.

different positions of these species in relation to such important factors as amount of available food and pressure of "diffuse" competition. *Tracheloraphis* species actually do not compete with other species, because their feeding spectra are rather specific. This results in ample opportunity for coexistence of these species. On the contrary, *Remanella* species and especially *Histobalantium* species are affected not only by competing pressure of trophic siblings, but also by that of other species with similar diet. This circumstance may intensify the competition between main competitors and promote their divergence.

Dependence of distribution overlap on total density of potential competitors

An overlap between related species in space and time evidently does not prove the fact of competition. Considerably overlapping species may either compete for common resource or jointly use it without influencing each other. However, this may be resolved if one establishes the spatial or temporal shift of one species under the influence of another. We found such a shift when studied the microdistribution of related species in homogeneous environment (on a horizontal plane), in highly heterogeneous but constant one (within sediments), and finally, as a result of total effect, in three dimensional space. In these cases, changes in relative positions of species in space did not depend on environmental factors. Although the shift in the species niche under influence of another (or several other) species can not be considered as a strict evidence of competition, it is certainly a strong argument in favour of it. To prove a competition, it is necessary to show that this shift is accompanied by reduction of ecological efficiency of the species, for example, the shift should lead to decrease in species density. This is partly shown in Fig. 1, but in that case the process of niche changing occurs in unstable environment. In microspace, under the stable conditions, interactions between related species quite often lead to their complete divergence ($a_{ij} = 0$) within given volume of space, but they never terminate in exclusion of one species by another. Interacting species eject each other to specific habitats (i.e. to the opposite points of gradient). With increasing the density of *Histobalantium majus* or *Remanella margaritifera* which prefer the most upper layers of sediments, their trophic analogues shift to deeper layers. The higher is the species density, the smaller is the zone of coexistence. Thus, evidences of interspecific competition can be easily found only in the case of high intensity of this process. More often one can observe situations, in which potential competitors occur together and utilize all available resources. In this case, the interspecific competition does not exceed the intraspecific one for both species. Curves shown in Figs. 4-6 reflect the dependence of spatial overlap between potential competitors on their total density according to data on horizontal (under the area of 10 cm^2), vertical (at the depth of 0-3 cm), and three dimensional distribution. In all these cases, an overlap decreases as the total density increases; this can be treated as a consequence of strong interspecific competition. When we consider horizontal and vertical distributions of species separately, this dependence is linear within broad range of total densities. Observed exceptions correspond to very low values of density (less than 10 ind/cm^2). In such cases, there is a positive linear dependence of overlap between each pair of species on their total density; this is conditioned by increasing the probability of encounters of individuals belonging to different species in dispersed populations. When we consider the distribution in three dimensional space, the revealed dependence becomes more complex: as population densities of both species increase, the overlap between them rises up to its maximum value which is specific for each pair of species, and then declines gradually approaching zero. Complete separation of habitat niches of particular species is observed at different population densities. Such separation between *Histobalantium* species takes place in homogeneous abiotic environment at the total density of 80 ind/cm^2 (at intersection of the line with abscissa in Fig. 1), in environment with Eh-gradient — at 32 ind/cm^2 and in three dimensional space — at 20 ind/cm^2. For species of *Tracheloraphis* and *Remanella*, such density values are 100, 85 and 80 ind/cm^2, and 400, 370 and 340 ind/cm^2, respectively. Although these values were obtained under particular conditions in 1987, we think that they reflect the degree of dissimilarity between considered pairs of species. The graphs given in Figs. 4-6 allow to judge about the intensity of competition between related species as well. It is generally higher in species of *Histobalantium* and lower in species of *Tracheloraphis*. The latter species did not reach the local density in 1987, at which the exclusion could be observed. Differences in intensity of competition between species with equally overlapping trophic niches, as it was noted above, are determined by different pressure of "diffuse" competition and by degree of food shortage.

One of competing congeneric species, as a rule, exerts greater influence on the partner than another does. We can judge about the competitive

ability of such species by their capacity to maintain high population density, to hold their own territories, or even to colonize the territories of other species. Basing on these criteria, we can consider the following species as the most strong competitors: *Tracheloraphis incaudatus, Remanella margaritifera* and *Histobalantium majus.* Competition advantage of *Remanella margaritifera* and *Histobalantium majus* is provided by their spatial position: occupying the most upper layers of sediments, these species are close to productional photic zone (0-2 mm), and under conditions of deficiency in food they able to completely block the food flow into deeper layers. However, when for some reason (e.g. because of low temperature or oxygen deficiency at the beginning of summer) the densities of these species are rather low, their nearest relatives occupy the dominant position (see Fig. 1). Thus, the mechanism of extinction of former species is the exceeding the tolerance threshold while that of latter species consists in the suppression by stronger competitors. The observations in nature are confirmed by field experiments, in which the removal of strong competitors from the community in late summer leads to increase in density of their close relatives (Burkovsky and Azovsky 1985).

In general, the species are more successful which more completely use all available resources during the season and, at the same time, less compete for them. In given community, *Tracheloraphis incaudatus, Histobalantium majus* and *Remanella margaritifera* are such species.

Conclusions

1. In the community of marine psammophilous ciliates, potential competitors coexist due to partial or complete divergence in space and time. This segregation is explained mainly by their different response to some environmental factors. Species differ by different positions in the sediments (along redox-gradient) to a greater degree than by divergence in horizontal distribution or in time.

2. When overlaps between feeding spectra (trophic niches) are equal, particular pairs of potential competitors are characterized by different overlaps in space. This is connected with the intensity of competition between them which depends on the amount of available food and the competition pressure of other species ("diffuse" competition).

3.Complete spatial exclusion of species occurs at certain population density which is specific for each pair of competitors. There is a linear dependence between spatial overlap along each axis of dimensions and the species total density. In three dimensional space, this dependence is more complex due to additional possibilities for species divergence.

4. The rank of abundance of a species is determined by its competition for food and space with all species in community, i.e. by the "diffuse" competition. Of two allied species, the species characterized by smaller overlap with other species of community and occupying the habitat closer to main food source (productional photic zone) is the superior competitor.

References

Burkovsky, I.V., 1984. Ekologija svobodnozhivushchikh infusorij. (Ecology of the free-living Infusoria). Moskva (in Russian).

_____.1987. Ecological resources partitioning and interactions of species in the community of marine psammophilous infusorians. Zoologicheskij zhurnal **66**: 645-654 (in Russian).

Burkovsky, I.V., and A.I. Azovsky. 1985. On correlation between the species number and stability in a community of marine psammophilous ciliates. Zoologicheskij zhurnal **64**: 813-819 (in Russian).

Burkovsky, I.V., A.I. Azovsky, and N.N. Moliboga. 1983. Diurnal vertical migrations of marine psammophilous infusorians of the White Sea. Zoologicheskij zhurnal **62**: 944-947 (in Russian).

Burkovsky, I.V., and V.S. Epshtein. 1982. Additional data on food specialization and trophic structure of the community of marine psammophilous infusorians. Zoologicheskij zhurnal **61**: 129-132 (in Russian).

Burkovsky, I.V., V.S. Epshtein, and N.N. Moliboga. 1980. Food specialization and trophic structure of the community of marine psammophilous infusorians. Zoologicheskij zhurnal **59**: 325-334 (in Russian).

Hairston, N.G., J.D. Allan, R.K. Colwell et al. 1969. The relationship between species dispersity and stability: an experimental approach with Protozoa and Bacteria. Ecology, **49**: 1091-1101.

Pianka, E.R. 1974. Niche overlap and diffuse competition. Proceedings of National Academy of Sciences, USA **71**: 2141- 2145.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science **185**: 27-39.

Vandermeer, J.H. 1969. The competitive structure of communities: an experimental approach with Protozoa. Ecology **50**: 362-371.

Vandermeer, J.H. 1970. The community matrix and the number of species in a community. American Naturalist **104**: 73-83.

Условия сосуществования потенциальных конкурентов в сообществе морских псаммофильных цилиат

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На песчаной литорали Белого моря изучали взаимное распределение трех пар таксономически близких видов цилиат: *Tracheloraphis incaudatus, Tr. phoenicopterus, Remanella margaritifera, R. rugosa, Histiobalantium majus, H. marinum.* Поскольку перекрывание трофических ниш (оцененное индексом Пианки) особенно велико для представителей одного рода (0.94 для видов рода *Tracheloraphis*; 0.94 для *Remanella*; 0.96 для Histobalantium), основное внимание было уделено обстоятельствам, допускающим возможность сосуществования этих видов.

Показано, что сосуществование возможно благодаря частичному расхождению видов в пространстве и во времени, обусловленному прежде всего их неодинаковым отношением к некоторым факторам среды. В наибольшей мере виды расходятся в толще грунта по вертикали (на градиенте редокс-потенциала), в меньшей степени — во времени и в наименьшей — по горизонтали на небольших расстояниях (в относительно однородной среде). Между величинами перекрывания видов по одной из осей пространства и их общей плотностью существует обратная связь. В трехмерном пространстве эта зависимость имеет более сложный характер: полное расхождение видов (взаимоисключение) наблюдается при плотности, специфической для каждой пары конкурентов. Ранг вида в сообществе определяется успехом его в конкуренции со всеми остальными видами за пищу и место. Более конкурентноспособным в каждой паре оказывается вид, имеющий меньшее перекрывание с остальными видами сообщества (испытывающим меньшее давление "диффузной" конкуренции) и ближе расположенный к основному источнику пищи (к фотической зоне).